Entry Behavior of the Crab *Pinnotheres maculatus* Say

Anne Eidemiller

The pea crab, *Pinnotheres maculatus* Say, inhabits the mantle cavity of the bay scallop, *Aequipectin irradians concentricus* Say. It is also reported in the literature from the sea pen, *Atrina rigida* Solander. The range of the scallop extends along the Atlantic coast of North America from Nova Scotia to Florida and along the Gulf Coast.

The purpose of the present study was to observe and study the behavior of the crab as it attempts entry into the scallop, and to investigate certain stimuli and responses in terms of possible relevance to the crab's ability to effect entry. In previous work done on the relationship, Sastry and Menzel (1962) report that the crab is attracted to the scallop by chemotactic stimuli, and that the crabs are negatively phototactic. Yeater (1966) studied the crab's choice of host when allowed to choose between *A. i. concentricus* and *Atrina rigida*. He found evidence that their preference of a host is influenced by water temperature since the adult crabs chose sea pens at tempeatures below 22 degrees C. and scallops at higher temperatures. This was related to the seasonal distribution of the scallops which disappear from the grass flats in colder weather when the sea grass dies off. He also found that the crabs exhibited a positive rheotaxis. The present studies represent a continuation of this work.

Christensen and McDermott (1958), using *Pinnotheres ostreum* Say, have traced the life history of the crab. Several larval stages are passed through in the plankton followed by the intial non-planktonic first crab stage at which time they become invasive. The invasive stage is characterized by a flat, hard carapace, flattened pereiopods with swimming hairs on the third and fourth pairs, and relatively well developed eyes and chelae. This stage is followed by several pre-hard developmental stages that are passed through within the host during which the crab shows modifications adapted to life within the host: a soft, rounded carapace, undeveloped tubular pereiopods and reduced chelae and sensory structures. The crab then enters the hard crab stage or sexual stage in which they again show the modifications associated with a free living existence. At this stage, the male

crab leaves its host and locates a female within a scallop where copulation occurs. The male does not develop beyond this point, but the female passes through five post-hard stages, the fifth being the adult which again shows all the modifications associated with the life within the scallop. It is this fifth stage crab that releases the larvae.

Materials and Methods

These studies were performed using *A. i. concentricus* Say infected with invasive stage and adult females of *P. maculatus* Say shipped from the Gulf Specimen Company of Panacea, Florida. A total of 83 scallops, 37 invasive stage crabs, and 18 adult female crabs were used. Trials were conducted in synthetic sea water at temperatures between 18 and 27 degrees C. The salinity varied slightly due to evaporation but remained within the range of tolerance of these animals. Water temperature was recorded during each trial. The crabs were removed from their hosts and placed in a holding aquarium and scallops were placed individually in finger bowls. Data are based on both observations and experiments in which both invasive and female stage crabs were involved.

Entry Behavior. The normal entry pattern of the crab and the response of the scallop was observed. In each observation, the scallop was placed into a large finger bowl containing 1.5 L of water and allowed to remain until the valves opened. As soon as it opened, a crab was placed in this bowl and the subsequent behavior of both noted.

Establishment and Maintenance Behavior. These studies involved the presentation of a stimulus and observation of the responses of experimentally altered and control crabs. Intact invasive stage crabs were used as controls.

An apparatus was constructed in order to test invasive stage and female crabs for rheotactic responses that might be involved in the establishment of the relationship. In this apparatus, a water current was siphoned through an inlet tube into a rectangular metal test chamber 24 cm long and 17 cm wide. The substrate consisted of aquarium gravel at a level 1.5 cm below the inlet tubing. The water depth was 5.5 cm. The strength of the

current could be regulated by means of two screw clamps on the inlet tubing.

To conduct a trial session, the chamber was allowed to fill with water until it began to overflow through the outlet spout at the opposite end of the chamber from the inlet tube, and the rate of flow was adjusted. Invasive stage and female crabs were then introduced into the chamber in a random fashion. The position of the animals was periodically observed, and the trial session terminated when distribution of the crabs remained stabilized for five minutes.

Crabs were tested for thigmotactic responses that might be involved both in the establishment and in the maintenance of the relationship. To investigate the relevance of thigmotactic responses to the establishment of this relationship, the ability of invasive stage crabs with impaired tactile senses to enter the scallop was compared to the ability of control crabs to effect entry. Both crabs were placed on the left valve of the scallop and the first entry attempt was recorded as that of a treated or a control crab. To impair the tactile sense of an experimental crab, the animal was daubed with gauze soaked in 10 per cent HCl; the daubing was repeated with gauze soaked in tap water. The crab was then placed in sea water and allowed to recover. This procedure did not destroy the sensory hairs of the crab since they remained visible under a dissecting microscope, but it did produce animals which, after recovering, did not respond to a tactile stimulus. Crabs were not used until 24 hours after being treated with acid in order to insure that their responses would not be affected by the treatment except to impair their tactile senses. Care was taken not to bring the HCl into contact with the eyes, antennae or antennules. Such crabs will be hereafter referred to as "touchless" crabs. To establish the role, if any, of thigmotactic responses in maintaining the relationship, the behavior of isolated untreated invasive stage crabs was observed with reference to their distribution in the holding aquarium. In addition, their response to a loose substrate of coarse aquarium gravel was noted.

An effort was made to determine if visual image stimuli and phototactic responses are involved in both the establishment and maintenance of the relationship. Phototaxis is here used in the

sense of a simple movement toward or away from light while visual image responses refer to those responses related to intact eyes in an environment where the intensity of the illumination did not vary.

To test the role of visual stimuli in the establishment of the relationship, invasive stage crabs were blinded by cauterization and allowed 24 hours to recover. A blinded crab was placed in a bowl with a scallop as was a control crab, and a record was made of which crab moved underneath the scallop shell first and remained there.

In order to test the role of phototactic stimuli in maintaining the relationship, a small glass aquarium, 23 × 16 × 14 cm, was employed. One half of the aquarium was covered on the sides, bottom and top with black construction paper and an electric lamp shone onto the other end, thus creating a sharp contrast between light and dark from one end of the aquarium to the other. The incidence of light on the darkened surface measured one foot-candle, while it measured 70 foot-candles on the illuminated surface. The crabs, untreated invasive stages and females, were placed in the aquarium at the boundary between light and dark, and their distribution at the end of the trial was noted. Trials were terminated when a stable distribution appeared to have been reached.

RESULTS

Entry Behavior. The behavior exhibited by a scallop during an entry attempt can be said to consist of four parts: (1) the mantle gapes apart at the point where the crab's legs touch it; (2) the scallop then opens to its fullest extent (this varies with the size of the scallop but is typically about 4 cm from shell margin to shell margin ventrally); (3) the scallop then closes abruptly but not completely as the margins usually do not make contact (the closely usually stops, leaving about 1 cm between the valves); (4) the scallop then reopens within five seconds.

In instances of successful entry, the scallop continues to open and close violently for so long as the crab remains on mantle tissue. Once the crab moves off the mantle tissue, the scallop ceases to react.

The stimulus to which the scallop reacts is basically a tactile one. The scallop shows no response until the crab makes physical

contact with the mantle, and the same response can be obtained by stroking the mantle with a blunt probe. Furthermore, a crab held in front of the mantle, opposite the ocelli but not in contact with the mantle, elicits no apparent response. The mantle is most sensitive on the region of the short guard tentacles. The observed gaping of the mantle results when the mantle edge curls out and back from the edge toward the point of contact of the crab.

Gutsell (1931) described the tactile sensitivity of the long extensible tentacles of the mantle, but in the course of the present studies, it was not always evident. If a crab was located on the margin of a valve or in the bowl beside the scallop and one of these tentacles made contact with it, the scallop did not react in any obvious way.

The behavior displayed by the crab in making entry attempts is not complex. The crab usually launches an entry attempt from the right or bottom valve, though it does make successful entry attempts from the left or upper valve if placed on that valve. Only one attempt was actually made from the upper valve in trials where the crab was free to approach and mount from any direction, and in this attempt, the crab approached the scallop dorsally. In all other attempts, the approach was ventral and lead to the crab moving onto the lower valve.

Successful entries are made as the crab moves over the margin of the shell laterally, thus touching the mantle first with either right or left pereiopods. The stimulus evokes the scallop's response, during which the crab is able to crawl quickly into the mantle cavity. If the crab does not achieve entry, it remains clinging to the margin of the shell until the scallop reopens, when it again attempts entry. The above descriptions are based on eight successful entry attempts by invasive crabs.

Three females were also observed in entry attempts. There was no difference noted in the behavior, and all three attempts were successful.

Establishment and Maintenance Behavior. In the rheotactic trials, it was noted that the crabs tended to congregate in that area of the test chamber that was behind the inlet tube opening, moving against the current, showing positive rheotaxis, to reach

that area. This inlet area constituted only 15 per cent of the total area available to the crabs. Four experimental sessions were run in which the crab distribution was recorded in terms of how many crabs concentrated into this rear area. Female and invasive stage crabs were tested together, but their distribution was recorded separately. The total trial length was 45 minutes. A total of 27 invasive stage crabs and 13 females were used.

There was a 100 per cent response for females and an 81 per cent response for invasive stage crabs. In addition, two sessions were run in which invasive blind crabs were used, with three crabs in each session for a total of six trials. There was a 100 per cent positive response. The average time of the blind crab trials was 25 minutes. Four trials were run in which touchless crabs were tested, and none migrated to the inlet area.

The results of the tactile trials are as follows. In ten out of twelve trials, the control crab made the first attempt, in one trial the touchless crab made the first attempt, and in one trial no entry attempt was made. In three trials of the 12, the touchless crab fell off the scallop altogether. In eight of 12 trials, both crabs placed on the same scallop at the same time, but no interaction was noted, probably owing to the tendency of touchless crabs to remain motionless. The average length of these trials was 20 minutes.

In addition to the above experimental data, the strength of the thigmotactic response in isolated female and invasive crabs was readily noted. In the stock aquarium, the isolated crabs were always aligned along the sides, and frequently three or four crabs were found to have aggregated in each corner. Also, if crabs were placed in coarse gravel, they tended to bury themselves in it. Invasives and females showed this response equally strongly.

The data from the vision and phototactic trials is as follows: in 26 trials to test the role of vision in establishing the relationship, the blind crabs moved underneath first in 12 or 46 per cent of the trials. The control crabs moved under first in six or 23 per cent of the trials. But in eight trials, or 30 per cent, neither crab moved under a scallop and remained there. The length of these trials averaged three and a half hours.

Eleven trials were run, five with blinded crabs and six with controls, in which the time required for each crab to move under the scallop and remain there was recorded. On the average, the control crabs required 4-8 minutes, compared to 12 minutes for blinded crabs. That is, the average the blinded crabs was two and one-half times that of the controls. These trials were run using a total of six blinded crabs.

In five sessions to test phototactic responses, a total of 54 trials were run, of which 34 involved the use of invasive stage crabs and 20 involved the use of mature females. The females moved into the dark and stayed there in 95 per cent of their trials, and the invasive crabs moved into the dark and remained there in 85 per cent of all their trials. Thus the total phototactic response was that 89 per cent of all crabs tested moved into the dark and remained there.

Discussion

These studies have been qualitative and in the nature of a preliminary survey of behavior and responses pertaining to the establishment and maintenance of the symbiotic relationship. Stimuli were investigated and responses observed, but no attempt was made to determine the relative importance of each of the stimuli involved or the sequence in which they act.

Entry Behavior. The crab showed no elaborate ritualized behavior in entering a scallop. The crab merely brings its pereipods into contact with the mantle and takes advantage of the scallop's response to enter the mantle cavity. The scallop's response favors entry of the crab since, by gaping the mantle and opening the valves further, it removes all mechanical barriers to the crab's entry. Furthermore, when the scallop closes, the frequent failure of the valves to meet at the margins allows the crab, if it has not already entered, to remain in the entry position and make another attempt. The scallop's rapid reopening is also to the advantage of a crab attempting re-entry. This behavior does not represent a specific response of the scallop to the stimulus presented by the crab since the same behavior can be evoked by the touch stimulus of a metal probe.

The gaping of the mantle is merely the curling of the outer, more sensitive fringe toward the point of stimulus; the further

opening of the valves is always preliminary to their violent closing. The incomplete closing of the valves is not so readily explained, however. To some extent, the observed incomplete closure may be an artifact, the result of the reaction of the scallops to shipment and a different environment. And yet, the same scallops that did not close completely after entry of a crab did close completely and rapidly, and remained closed after crabs were removed from the mantle cavity, thus indicating their ability to close completely. Possibly, the tactile stimulus provided by the entering crab is below a minimum threshold of intensity for complete closure. The rapid reopening is probably related to incomplete closure since a positive correlation between degree of closure and length of time of closure was noted. Sastry (1961) reported that occasionally crabs were caught between the valves and injured.

Establishment and Maintenance Behavior.—The response to water currents was found to be relevent to the ability of the crab to locate a host which produces a distinct current through its filter feeding behavior. The female crabs showed a more complete response than did the invasives. The rheotactic and thigmotactic responses seem to be related since the crabs with impaired tactile senses did not react to the current. However, the smaller number of touchless crabs used was inadequate to fully establish this point.

The importance of tactile stimuli in directing the crab's entry attempt, once on the valve of the scallop, is thought to be clearly established in these studies. It appears that the positive thigmotaxis displayed by crabs is related to maintenance of the relationship, once established, in that this response acts to maintain the crab inside the scallop where it is in complete physical contact with the scallop's viscera. To move outside the scallop would remove this contact and thus be an action in opposition to the normal positive thigmotaxis.

The vision time trials indicate that vision plays a role in the crab's ability to locate a scallop. The inconclusive and somewhat contradictory results obtained in those trials dealing with the observations on which crab, blinded or control, moved under the scallop first could be due to the tendency of the blinded crabs to engage in a great deal of random swimming. In all trials in which

they were used, blinded crabs displayed this swimming, and this might explain the more rapid positive rheotaxis of blinded crabs in the current trials as well.

The negative phototaxis exhibited by these crabs is thought to act to maintain the relationship, since to leave the host means to move from the dark mantle cavity into the light which is the reverse of the normal response. In most of the trials, the females showed a stronger phototaxis than did the invasives. It may be recalled that they also showed a stronger rheotactic response. That the positive phototaxis is stronger in females which never normally leave the darkness of the mantle cavity is not surprising.

In addition to previously mentioned potential sources of error, the blinding of crabs by cauterization may have had physiological side effects that could have affected the crabs' behavior; the random swimming of blinded crabs, for instance, might be due to this.

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Department of Oceanography, Florida State University, Tallahassee, Florida.